

## PATTERNS OF WHOLE COLONY PREY CAPTURE IN THE OCTOCORAL, *ALCYONIUM SIDERIUM*\*

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### ABSTRACT

Colonies of a boreal octocoral, *Alcyonium siderium*, preferentially catch prey on specific regions of the colony at certain flow speeds of low turbulence. Colonies feeding on brine shrimp cysts capture prey preferentially on the upstream side of the colony under low flow conditions ( $2.5 \text{ cm} \cdot \text{s}^{-1}$ ). At intermediate flow speeds ( $9.0 \text{ cm} \cdot \text{s}^{-1}$ ), prey capture is uniformly distributed around the circumference of the colonies, while at higher flow speeds ( $19.0 \text{ cm} \cdot \text{s}^{-1}$ ), prey capture again becomes asymmetric and downstream polyps capture the most prey. At higher levels of free-stream turbulence, these asymmetric prey capture distributions around the colony disappear; in the vertical direction, prey capture is asymmetric over the surface of the colony at all flow speeds tested, with polyps nearer the top of the colony capturing the most prey only at the lowest speeds. Asymmetrical filtration results from (1) increasing mechanical deformation of polyps into an orientation unfavorable for prey capture with increasing flow speed, and (2) differential prey concentrations in the boundary layer of the colony in the downstream direction. For non-motile particles, the filtration performance of this passive suspension feeder appears governed only by the flow speed and turbulence, the mechanical behavior of the filter elements, and the motion of the particles in the boundary layer of the colony.

### INTRODUCTION

Organisms which rely on ambient water currents to bring them suspended particulate food are termed passive suspension feeders (Jørgensen, 1955) and are often the most conspicuous members of benthic communities. Passive suspension feeding is especially common in the phylum Cnidaria. Coral reef cnidarians may require periodic inputs of zooplankton to meet their nutritional requirements (Johannes *et al.*, 1970; Muscatine and Porter, 1977). Boreal cnidarians such as sea anemones, octocorals, and ahermatypic scleractinians rely almost exclusively on passive suspension feeding in obtaining food. Success in catching particulate prey can determine body size and mode of reproduction in sea anemones (Purcell, 1977; Sebens, 1981; Sebens and Koehl, 1984), and colony size in an octocoral (Sebens, 1984). Since passive suspension feeders are sessile, they must contend with potentially damaging hydrodynamic drag forces while filtering the water for food (Wainwright and Koehl, 1976).

Orientation to ambient currents can occur in passive suspension feeders as a result of their sessile habit. Cnidarians such as hydroids (Riedl, 1971; Svoboda, 1976) and octocorals (Théodor and Denizot, 1965; Grigg, 1972; Rees, 1972; Patterson, 1980) often orient the longest dimension of the colony perpendicular to the prevailing

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Abbreviations: K-S, Kolmogorov-Smirnov.

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flow. Such an arrangement permits the colony to intercept the greatest amount of prey per unit time (Warner, 1976). Maximization of food intercepted by prey-capturing surfaces may underly the behavioral ecology of crinoids (Meyer, 1973; Macurda and Meyer, 1974), and ophiuroids (Warner, 1971; Warner and Woodley, 1975), as well as sea anemones (Robbins and Shick, 1980). Hermatypic scleractinians also display orientation to currents and surge. In some species, the shape of the colony enhances water flow through the branches (Abbott, 1974); in others, orientation minimizes the bending stresses in the larger branches of the colony (Chamberlain and Graus, 1975; Vosburgh, 1977).

Orientation to flow is a well-studied phenomenon in passive suspension feeders, yet few studies have examined how prey capture occurs at either the polyp or whole colony level. While the prey caught in the field by passive suspension feeders have been described and quantified [e.g., corals (Porter, 1974), zoanthids (Sebens, 1977), sea anemones (Purcell, 1977; Sebens, 1981), soft corals (Sebens and Koehl, 1984)], there are few quantitative descriptions of prey capture mechanisms (Koehl, 1977; Lasker, 1981). A step towards a quantitative theoretical understanding of how biological filters work was taken by Rubenstein and Koehl (1977). They suggested that the engineering theory of aerosol filtration could serve as a possible unifying scheme for biological filtration. They demonstrated that all biological filters need not act like simple sieves as previously tacitly assumed, but that there are at least five possible mechanisms for particle capture at the level of the filtering element. They also showed how, for simple filter element geometries, the theory allowed predictions of filtration efficiencies for the different mechanisms. LaBarbera (1978) subsequently applied the theory of aerosol filtration to passive suspension feeding in an ophiuroid and found excellent agreement between his results and the predictions of particle collection efficiency calculated using the theory. However, a more recent review (Jørgensen, 1983) of the applications of aerosol filtration theory to suspension feeding indicates that more work needs to be done on determining the limits of applicability of some of the concepts, especially on how direct interception functions as the dominant mode of particle capture (LaBarbera, 1984). The role of particle loss after capture and the surface properties of biological filters are liable to be the areas which can explain the deviations of theory from observation.

How important are the spatial arrangements of *assemblages* of filter elements (i.e., colonies or tentacle crowns), in determining local flow patterns? What effect does flow over a filter have on the motion of a passive food particle in the boundary layer of the organism? Patterns of flow around benthic invertebrates have only recently been studied in scleractinians (Chamberlain and Graus, 1975), hydroids (Svoboda, 1976), sand dollars (O'Neill, 1978; Telford, 1981), brachiopods (LaBarbera, 1981), and zoanthids (Koehl, 1977), and have been shown to have important implications for feeding behavior and shape in these organisms. Leversee (1976) studied whole-colony feeding in gorgonians and assumed the same first order feeding rate model previously used to describe *active* suspension feeding (Jørgensen, 1949). His study clearly demonstrated the importance of *in situ* orientation to prevailing currents, and indicated the asymmetric nature of food capture (downstream side of colony). Capture of prey on the downstream side of the colony has also been observed by Lasker (1981) in gorgonians and by Porter (1979) in scleractinians. Okamura (University of California, Berkeley, pers. comm.) recently discovered that success in prey capture by individual zooids in an erect bryozoan is dependent on both location on the colony and flow speed. But in general, patterns of prey capture of sessile suspension feeders have not been investigated under controlled experimental conditions, and thus it is difficult to interpret the few patterns that have been reported.

A passive suspension feeder which is locally abundant in the New England subtidal is the colonial soft coral, *Alcyonium siderium* Verrill, a zooplanktivore (Sebens and Koehl, 1984). Little is known about it other than work on gametogenesis (Feldman, 1976), larval ecology (Sebens, 1982, 1983a, b, c), and the composition of prey taken in the field (Sebens and Koehl, 1984). Colonies often have simple geometries [spheroids, ellipsoids, cylinders; Patterson (1980)] which simplifies many experiments addressing flow patterns and locations of prey capture. Colonies also occur on shells of the horse mussel, *Modiolus modiolus*, and this facilitates their use in laboratory feeding experiments. Prey capture of zooplankton in the field and laboratory can be observed with the naked eye as the tentacles of this species measure approximately 3 mm (Sebens and Koehl, 1984) and contract in a characteristic fashion toward the pharynx after catching a zooplankton. It was possible to measure success in prey capture over colony surfaces after short feeding bouts in the laboratory, and to quantify the effect of flow speed and turbulence intensity on this process.

### MATERIALS AND METHODS

All laboratory experiments were conducted at the Marine Science and Maritime Studies Center (MSMSC), Northeastern University, Nahant, Massachusetts, where colonies of *Alcyonium siderium* were collected monthly and maintained in flowing sea water tables. A recirculating flow tank was constructed from plexiglas, patterned after a design published by Vogel and LaBarbera (1978) and was used in feeding experiments. Center channel midwater flow speeds in the working section [12 cm (depth)  $\times$  16 cm (width)  $\times$  75 cm (length)] were continuously variable between 0 and 40  $\text{cm} \cdot \text{s}^{-1}$ . Volume of the system when full was about 98 l. Shear velocity ( $U^*$ ) was calculated by regressing average flow speed at a height ( $z$ ) versus  $\ln z$ , and could be set as high as 1.6  $\text{cm} \cdot \text{s}^{-1}$  if no turbulence reducers (Hexcel flow straighteners, cell diameter = 1.0 cm) were used. When the Hexcel flow straighteners were removed from the upstream section of the tank work area, the level of turbulence increased and mean flow speed profiles became steeper, approximating the hydraulically rougher flow seen by these organisms in the field.

The impeller used to push water through the tank was driven by a Bodine NSH-12 1/50 hp DC motor controlled by a Bodine ASH-500 solid state speed control. Variation in motor speed was less than 2%. Sea water was obtained from the MSMSC sea water system and was filtered twice (sand, cotton mesh) to remove particles greater than 20  $\mu\text{m}$  in diameter.

Flow speeds and turbulence intensities (see Bradshaw, 1971, for a discussion of turbulence and its measurement) were measured with a two channel thermistor flow-meter circuit (LaBarbera and Vogel, 1976). This device was contained in an underwater housing (Ikelite #4610) for *in situ* field measurements. Data were recorded as an FM signal on a microcassette tape recorder (Olympus Pearlcor S802) with high-quality microcassette (Olympus MC-90-AR); a tape speed of 1.2  $\text{cm} \cdot \text{s}^{-1}$  allowed continuous recordings of up to two hours in the laboratory and field. Recordings were read from the tape into an Apple IIe microcomputer via a signal conditioner (custom-made) and 8 bit successive approximation A/D convertor (Mountain Computer) at a sampling rate of 10 Hz. Seven points were used in the regression calculations of shear velocity using ensemble averages. Flow speed profiles and turbulence intensity were measured 10 cm upstream of the colonies tested (see Fig. 2).

Mussels (*Modiolus modiolus*) with octocoral colonies were collected from the subtidal using SCUBA. In the laboratory, the mussel shells were fractured, and shell fragments with single colonies were cut using tin snips.

*Alcyonium* readily catches and ingests hydrated *Artemia* cysts. Hydration of desiccated cysts occurs in less than 30 minutes (hydrated mean diameter  $210 \pm 15 \mu\text{m}$  S.D.;  $n = 100$ ), and they were almost neutrally buoyant. Cysts did not change size significantly during the first four hours of use ( $t$ -test;  $P < 0.05$ ;  $n = 100$ ). The cysts are within the size range preferred by *Alcyonium* in the field (Sebens and Koehl, 1984). They were easily seen in the translucent coelenteron of polyps for up to 12 hours after capture.

#### *Location of prey capture*

The spatial position of prey capture on colonies with bilaterally symmetric geometries was studied in flows of low and high turbulence levels and differing mean flow speeds. Colonies ranged in size from 2 to 8 cm in greatest dimension when expanded and generally approximated bilaterally symmetric ellipsoids and spheroids. Prior to the start of a feeding bout, a single colony was introduced to the flow tank and allowed to acclimate to the flow regime selected for the experiment and to expand its polyps fully. A standard volume of sea water (1.5 l) and hydrated cysts were added to the flow tank all at once at the start of the bouts which lasted 10 minutes. About five minutes into the experiment, three 60 ml samples were withdrawn isokinetically (Parker, 1968; Hewitt, 1978) from the flow using a Cole-Parmer peristaltic pump (model no. 7568) smoothed with hydraulic capacitors. Tests indicated that appreciable settling of the cysts did not occur throughout the duration of the experiment. Samples were filtered onto gridded Millipore filters, the number of cysts was counted, and a mean concentration of particles present in the flow was calculated.

At the end of each feeding bout, the flow was stopped and capture sites of cysts on the colony were mapped. Side projections and censuses were made by moving the colony to the side of the flow tank and mapping capture sites directly on the clear plexiglas tank wall with a felt-tip pen. The maps were then transferred to tracing paper; this side view mapping was only performed for feeding experiments with the flow straighteners removed. Top projections of colonies were made by removing colonies from the tank and transferring them to a small bowl. The top projection of the colony and location of caught particles were traced on a clear plastic sheet suspended over the bowl. The transfer of the colony out of the tank did not result in the loss of any prey items already inside the coelenteron. This procedure necessarily missed particles on the underside of the colonies in top projections and the backside of colonies in side projections. Figure 1 shows a typical top and side view of a colony after a feeding bout, with the coordinate system used to assess location of capture.

Areas of projected colony surfaces were measured using an Apple Graphics Tablet digitizer with a linear resolution of 0.1 mm. The digitizing tablet was also used to locate the centroid of top projections, and an angular coordinate system for these projections was established using the centroid and direction of flow past the colony (see Fig. 1). Twelve angular sectors of 30 degrees each were established for each colony and the data for the bilaterally symmetric halves were pooled for analysis. Side projections were divided into five non-dimensional length sectors (see Fig. 1). Particle counts in each angular or length sector were normalized by the projected total area available for particle capture.

#### *Polypal deflections in flow*

The deflections of individual polyps at various angular positions around a colony surface in different flow regimes were measured by one of two methods. Deflections

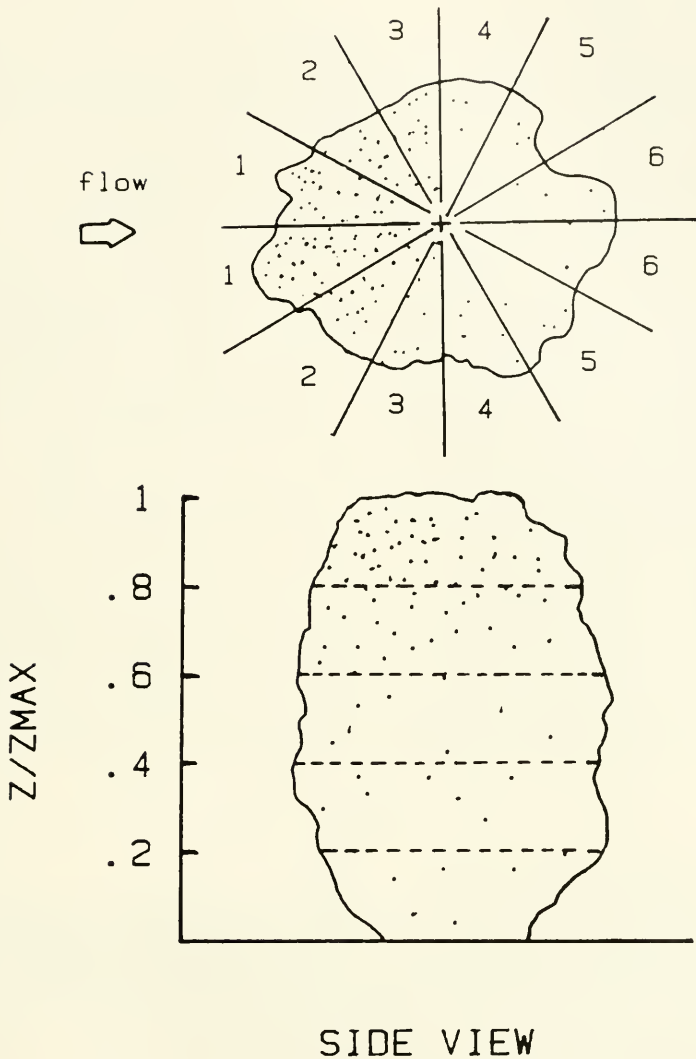


FIGURE 1. Particle capture sites on a typical *Alcyonium* colony. The upper figure is a vertical projection divided into bilaterally symmetric 30 degree sectors, with 0 degrees upstream and 180 degrees downstream. The dots indicate sites of prey capture, the cross indicates the centroid of the projected area in the top view, and the arrow indicates the direction of flow. The lower figure is a lateral projection showing the dimensionless five sector height coordinate used.

at lower speeds were measured directly through a dissecting microscope with micrometer ocular suspended above the flow tank. At the higher flow speeds tested, deflections were measured on tracings made from films of colonies in flow. Films were made using a Minolta XL 401 Super 8 mm movie camera with macro lens and were single-frame projected onto tracing paper. Deflections were measured to the nearest 0.1 mm with either scheme. In both types of experiments, polyps were carefully chosen to be those deflecting in a plane parallel to the focal plane of the camera.

### *Boundary layer particle concentrations*

Concentrations of particles in the boundary layer of the colony are difficult to measure without employing sophisticated and expensive techniques such as laser-doppler anemometers (Lee and Srinivasan, 1978; Bunimovich and Kudin, 1982). However, I measured particle concentrations integrated over periods of minutes at various angular positions around a colony using a dissecting microscope suspended over the working section of the flow tank. A magnification of 50X was used to observe the passage of cysts through a specified volume surrounding individual polyps (Fig. 4A). This cylindrical volume had a radius of 2.0 tentacle lengths and a height equal to the anthocodial stem height plus the tentacle height. Focal distance and magnification were adjusted so that the depth of field when checked with a printed scale on a ruler was equal to the diameter of the cylindrical volume. During timed 180 second intervals (T), particles in focus passing through the volume were counted (N). Thermistor flowmeter measurements of speed ( $U$ ;  $\text{cm} \cdot \text{s}^{-1}$ ) were then made at these same locations at the level of the tentacular surfaces. An estimate of the expected number of particles ( $N_e$ ) was calculated for each station, where  $N_e = A \times U \times C \times T$ , with  $C$  = ambient cyst concentration ( $\text{particles} \cdot \text{cm}^{-3}$ ), and  $A$  = projected surface area of the volume ( $\text{cm}^2$ ). All these measurements were made at a flow speed of less than  $5 \text{ cm} \cdot \text{s}^{-1}$ .

At higher flow speeds ( $>5 \text{ cm} \cdot \text{s}^{-1}$ ), it was not possible to determine reliably which particles were in focus and a different technique was used to estimate particle availability. Collimated beams of light were passed immediately upstream and downstream of the colony in flow in a darkened room and short time exposure photographs (1/8 s) taken. Cylindrical volumes were established and particle streaks beginning inside the volume were counted. Hence particle concentrations could be established directly using this technique. A check of this technique at low speeds indicated it gave the same results as those obtained using direct observations.

## RESULTS

### *Feeding experiments: low turbulence*

Experiments were first conducted in flows that did not show steep speed profiles or have high turbulent kinetic energy levels. The flow became hydraulically 'rougher' (Nowell and Church, 1979) when the flow straighteners were removed (see Fig. 2). Examination of patterns of particle capture for a colony in the less rough flow may offer insights into feeding observed in a hydraulically rougher flow.

Figure 3 depicts the results of experiments conducted at mean maximum flow speeds of 2.5, 9.0, and  $19.0 \text{ cm} \cdot \text{s}^{-1}$ . Percent data were arcsine transformed before calculation of statistics (Zar, 1974), and then back-transformed for graphical portrayal. Angular position of capture is markedly asymmetric at the lowest speed, with upstream polyps capturing significantly more prey than their downstream neighbors [Kolmogorov-Smirnov (K-S) goodness of fit,  $P < 0.01$ ]. At intermediate flow speeds, the distribution of prey cannot be distinguished from an even distribution (K-S,  $P > 0.10$ ), while at the highest flow speed tested, an asymmetric distribution again appears, with downstream polyps enjoying greater success in prey capture (K-S,  $P < 0.01$ ).

### *Boundary layer experiments*

Boundary layer measurements of particle availability in the downstream direction over a colony are shown in Figure 4B. At the flow speeds tested ( $<5 \text{ cm} \cdot \text{s}^{-1}$  at a

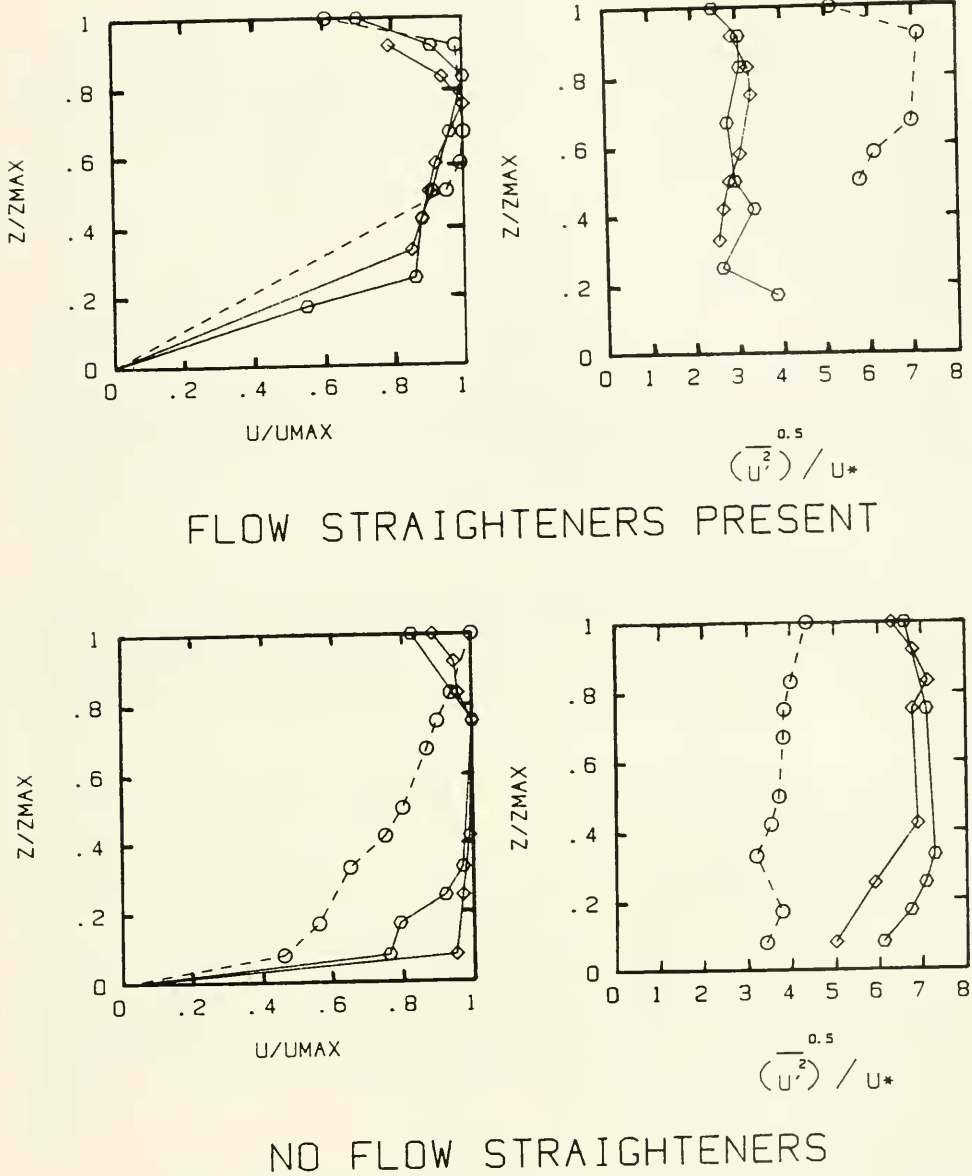


FIGURE 2. Flow regimes encountered by *Alcyonium* colonies in the recirculating flow tank with and without turbulence reduction. Left-hand graphs show flow speed ( $U$ ) profiles in a direction normal to the substrate, normalized to the maximum mean flow speed ( $U_{MAX}$ ). Right-hand graphs depict turbulent kinetic energy ( $\overline{U'^2}$ ) in the direction normal to the substrate, normalized to the shear velocity ( $U^*$ ). Height above the substrate ( $Z$ ) is normalized to the depth of the working section of the flow tank ( $Z_{MAX} = 12.0 \text{ cm}$ ). Note the effect of the flow straighteners on the steepness of the flow profile and the level of turbulence in the flow tank. With flow straighteners: circles ( $U_{MAX} = 2.5 \text{ cm} \cdot \text{s}^{-1}$ ;  $U^* = 0.2 \text{ cm} \cdot \text{s}^{-1}$ ), hexagons ( $U_{MAX} = 9.0 \text{ cm} \cdot \text{s}^{-1}$ ;  $U^* = 1.0 \text{ cm} \cdot \text{s}^{-1}$ ), diamonds ( $U_{MAX} = 19.0 \text{ cm} \cdot \text{s}^{-1}$ ;  $U^* = 1.6 \text{ cm} \cdot \text{s}^{-1}$ ). Without flow straighteners: circles ( $U_{MAX} = 2.7 \text{ cm} \cdot \text{s}^{-1}$ ;  $U^* = 0.3 \text{ cm} \cdot \text{s}^{-1}$ ), hexagons ( $U_{MAX} = 12.2 \text{ cm} \cdot \text{s}^{-1}$ ;  $U^* = 0.5 \text{ cm} \cdot \text{s}^{-1}$ ), diamonds ( $U_{MAX} = 19.8 \text{ cm} \cdot \text{s}^{-1}$ ;  $U^* = 1.5 \text{ cm} \cdot \text{s}^{-1}$ ).

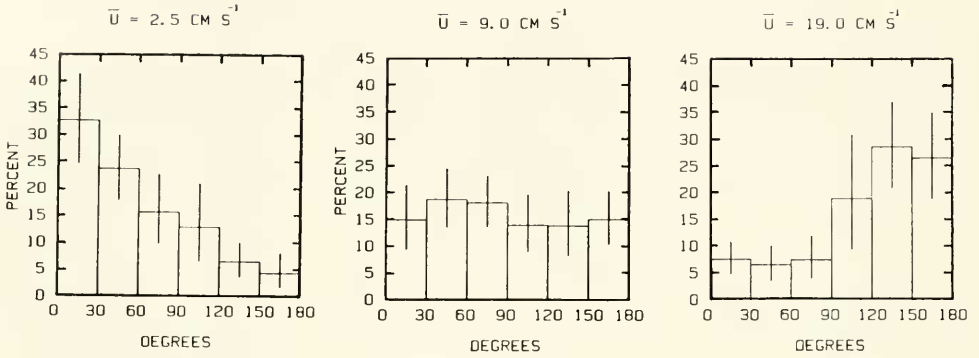


FIGURE 3. Angular position of prey capture events for low turbulence flow at three different flow speeds. Data from the bilateral halves of the colony are pooled; hence the abscissa runs from 0 to 180 degrees, with 180 degrees being the extreme downstream point. Capture frequencies have been normalized relative to the amount of area available for prey capture. Vertical bars are 95% confidence intervals. For flow speeds of 2.5, 9.0, and 19.0  $\text{cm} \cdot \text{s}^{-1}$ , the number of colonies fed were 12, 13, and 11, and the total number of cysts caught were 283, 425, and 186, respectively.

height of 5 cm), the concentration of cysts in the boundary layer of the four colonies tested showed a highly significant reduction in the downstream direction. Results of collimated light beam measurements are shown in Table I. At higher flow speeds ( $>9.0 \text{ cm} \cdot \text{s}^{-1}$  at a depth of 5 cm), this asymmetry in particle concentration disappeared. Concentrations of particles in the wake were no lower than those of the free-stream

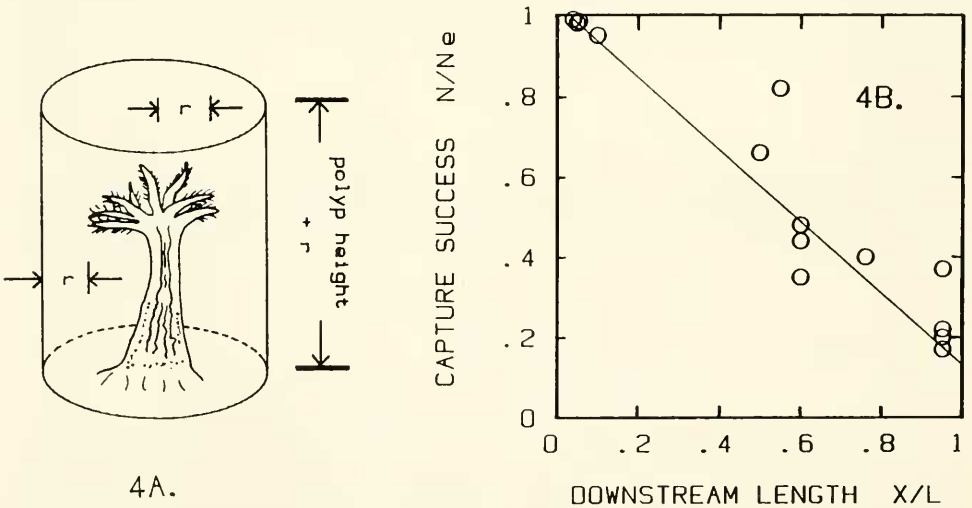


FIGURE 4. Boundary layer depletion measurements. (A) Volume used in boundary layer studies of feeding. Dimensions of the volume are indicated in the upper figure with  $r$  = radius of the oral disk. (B) Particles passing through the control volume were counted ( $N$ ), and compared with an expected value,  $N_e = A \times U \times C \times T$ , where  $A$  = projected cross-sectional area of control volume ( $\text{cm}^2$ ),  $U$  = mean flow speed  $2r$  above the tentacles ( $\text{cm} \cdot \text{s}^{-1}$ ),  $C$  = ambient particle concentration ( $\text{no.} \cdot \text{cm}^{-3}$ ), and  $T$  = counting period (s). The downstream length coordinate ( $X$ ) used to locate the position of polyps was measured in a curvilinear fashion around the perimeter of the colony, and was normalized by the overall length coordinate ( $L$ ) measured in the same fashion. The equation of the line fit by least-squares method to the data is  $N/N_e = -0.89 (X/L) + 1.03$  with  $R^2 = 0.88$ .  $T = 180$  seconds.

TABLE I

*Mainstream versus wake concentrations of Artemia cysts near a colony of Alcyonium as function of flow speed*

U ( $\text{cm} \cdot \text{s}^{-1}$ )	Delta concentration
0.9	-0.08 (0.22)
5.6	0.04 (0.22)
7.3	0.04 (0.47)
8.4	0.07 (0.41)
9.5	0.10 (0.27)

Concentrations measured photographically using beams of light immediately upstream and downstream of the colony. A positive mean delta C indicates that the concentration in the wake was higher than that in the mainstream. Values given are mean (S.D.) and have been normalized by the mean mainstream concentration during the experiments ( $414 \text{ cysts} \cdot \text{l}^{-1}$ ). All values are not significantly different from zero ( $t$ -test,  $P < 0.01$ ) indicating that concentrations of particles in the wake and mainstream were the same.

(Table I); in fact, they were slightly higher, although this difference was not significant ( $t$ -test,  $P < 0.01$ ).

Table II demonstrates that polyp deflections are greatest towards the upstream side of the colonies tested, with polyps in the wake experiencing little or no deflection. Deflections were greatest at the  $90^\circ$  angular position when the flow speed was strong enough to deflect enough upstream polyps out of the way of the flow. Figure 5 shows a profile of polyp movements from an experiment where the flow was increased from 0 to  $8.4 \text{ cm} \cdot \text{s}^{-1}$  over a small colony.

#### *Feeding experiments: higher turbulence*

The pattern of particle capture observed in a hydraulically rougher flow is shown in Figure 6. Note that the distribution of capture events at the three mean maximum flow speeds tested ( $2.7, 12.2, 19.8 \text{ cm} \cdot \text{s}^{-1}$ ) has lost the asymmetry seen in the less turbulent case. Distributions could not be distinguished from an even distribution of prey around the colony (K-S,  $P > 0.10$ ).

In the vertical direction, there was a significant tendency for colony sectors furthest from the substrate to catch relatively more prey at low speeds (Fig. 7) than sectors closer to the tank floor; at higher speeds, the distribution flattened out and then became significantly different from an even distribution at the highest flow speed tested (K-S,  $P < 0.05$ ), showing a bimodal distribution with polyps at intermediate height on the colony catching the least amount of prey on a per capita basis.

TABLE II

*Polyp deformation (d/L) versus flow speed (U)*

U ( $\text{cm} \cdot \text{s}^{-1}$ )	Angular position (degrees)		
	0	90	180
2.5	0.01 (0.02)	0.09 (0.07)	0 (0)
9.0	0.43 (0.42)	0.95 (0.08)	0 (0)
19.0	0.50 (0.16)	0.67 (0.17)	0 (0)

Angular position stations are measured relative to the centroid of the colony when viewed from above. Polyps in the wake moved back and forth in the turbulence, but had no net displacement. Values given are mean (stan. dev.).  $n = 8$  polyps per station.  $d$  = polyp tip deflection,  $L$  = polyp length.

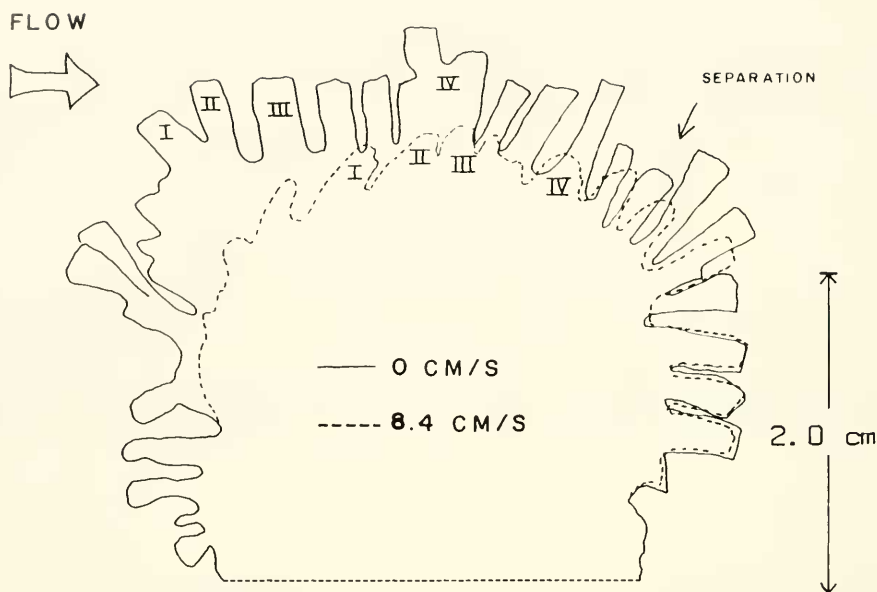


FIGURE 5. Deformation of polyps on the surface of a small colony is visible in this tracing made from a Super 8 mm film of the colony in still water and then in a flow of  $8.4 \text{ cm} \cdot \text{s}^{-1}$  measured at the level of the height of the colony 10 cm upstream. Note the lack of deflection of the polyps in the wake of the colony. The separation point was determined using a filament of dye.

## DISCUSSION

### Flow in nature

Colonies of *A. siderium* typically occur on shallow (<20 m depth) subtidal vertical rocky substrates with some colonies occurring on the undersides of boulders, on horizontal rock surfaces, and on *Modiolus* shells attached to rock. The flow envi-

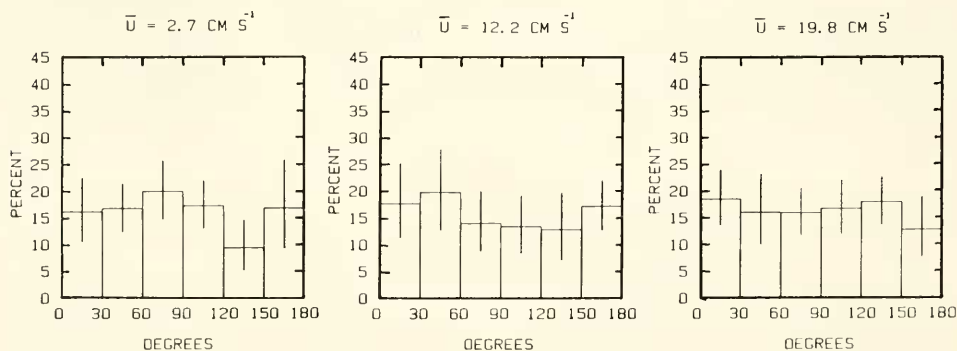


FIGURE 6. Angular position of prey capture events for increased levels of turbulence at three different flow speeds. Data from the bilateral halves of the colony are pooled; hence the abscissa runs from 0 to 180 degrees, with 180 degrees being the extreme downstream point. Capture frequencies are normalized relative to the amount of colony area (and hence number of polyps) available for prey capture. Vertical bars are 95% confidence intervals. For flow speeds of 2.7, 12.2, and  $19.8 \text{ cm} \cdot \text{s}^{-1}$ , the number of colonies fed were 10, 10, and 11, and the total number of cysts caught were 383, 305, and 747, respectively.

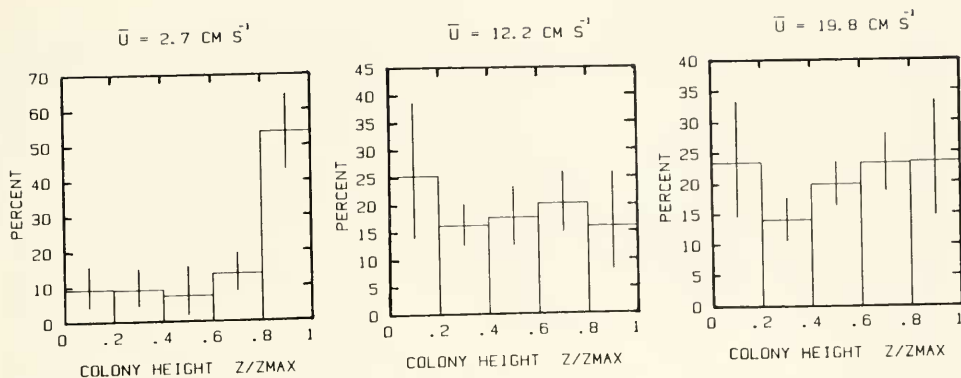


FIGURE 7. Vertical position of prey capture in three flows without turbulence reduction.  $Z$  is the distance above the substrate and it has been normalized to  $Z_{\text{MAX}}$ , the height of the colony. Capture frequencies have been normalized relative to the amount of area available for prey capture. Vertical bars are 95% confidence intervals. For flow speeds of 2.7, 12.2, and 19.8  $\text{cm} \cdot \text{s}^{-1}$ , the number of colonies fed were 11, 10, and 11, and the total number of cysts caught were 346, 342, and 687, respectively.

ronment encountered by passive suspension feeders in such habitats is apt to be quite complicated three-dimensionally. Waves entering the shallow water over these habitats induce oscillating flows which become more important the closer one moves toward any physical boundary in the flow, such as the bottom (Madsen, 1976). Such wave-induced surge can often be of the same order of magnitude as tidally driven currents, when time or ensemble averages of flow speed are made at these sites (Patterson, in prep.). The boundary layer near the bottom is further complicated by the presence of irregularities (sessile organisms, crevices, promontories, sand or mud, and boulders) called 'roughness elements' in the geophysical fluid dynamics literature (Nowell and Church, 1979), which can vary in their density and size distribution and in their effect on the turbulence intensity and character of the flow (Komar, 1976). The effect of distributed roughness elements on shallow water benthic communities has only recently been investigated (Eckman *et al.*, 1981; Nowell *et al.*, 1981; Jumars and Nowell, 1984). Turbulence, bottom shear stress, and water flow encountered by benthic invertebrates can vary a great deal on relatively small spatial scales (Eckman, 1983). The effects of upstream roughness elements are manifold, including the generation of boundary layers within boundary layers, further complicating description of the benthic environment; deeper water studies are attempting to gather empirical measures of roughness elements in the field through photogrammetry and scale models in flumes (Paola, unpub.).

The complications of flows in fully rough depth-limited boundary layers make interpretation of feeding experiments performed in a recirculating flow tank less certain, but it is valuable to compare experiments from the less realistic hydraulically smooth case to those where turbulent mixing may be of importance in understanding how natural flows interact with the passive suspension feeding process.

#### *Explanations for asymmetric capture*

The asymmetry of particle capture in *A. siderium* seen at lower and higher smooth flow speeds could arise from several effects (Patterson, 1983): (1) differential concentrations of prey near the surface of the colony may occur along the downstream coordinate. This effect might be expected to show some dependence on flow speed and turbulence level. Experiments with neutrally buoyant glass beads suspended in

laminar flows over flat plates indicate that particle concentrations in the boundary layer can become depleted in the downstream direction (Einav and Lee, 1973), and this effect *decreases* with *increasing* flow speed and turbulence. (2) The polyps and their prey capture surfaces, the tentacles, could experience changing degrees of deformation from flow-induced shear stress on the oral disk and form drag on the columns, which may lead to unfavorable orientations for prey capture at certain flow speeds. (3) The eddying wake on the downstream side of the colony changes in size and shape with changing flow speed and may affect prey capture for downstream polyps. Concentrations of particles in the wake may be different from those in the free stream (Lee and Srinivasan, 1978), and this may affect prey capture.

### *Particle concentrations in the boundary layer*

The first hypothesis is supported by experimental data (Fig. 4, Table I). Concentrations of almost neutrally buoyant brine shrimp cysts in the boundary layer of the colony decrease in the downstream direction at lower speeds. Calculations indicate that predation by upstream polyps can account for only 5% of the depletion observed, leaving hydrodynamic effects as the only mechanism possibly responsible for particle migration.

Observations made through a dissecting microscope at 50X indicate that particles are spinning in the shear field near the tops of the polyps; this rotation may be crucial in the generation of forces responsible for the movement of the particles away from the substrate. Particles that entered the colony below the level of the tentacles meandered downstream between the anthocodial stems, and appeared to be moving away from the surface of the colony the further they progressed downstream. An alternative but not mutually exclusive explanation for the depletion is that flow patterns over and through the polyp-studded surface of the colony aid in movement of particles away from the substrate. Visualization of the flow with filaments of rhodamine dye indicated that flow below the level of the tentacles was slow and laminar and that an abrupt transition occurred above the polyps in the character of the flow, with a steep velocity gradient present (Patterson, in prep.). This effect disappears at higher flow speeds and the availability of prey becomes uniform again (Table I).

The asymmetric capture of particles around the surface of the colony disappeared with increasing flow speed. Particles in flows of the scale considered here are influenced by both inertial and viscous forces (Saffman, 1965). Jørgensen (1982, 1983) has implicated shear-induced particle migration as a mechanism for particle capture in active suspension feeders such as molluscs. Detailed studies of the shear field and particle concentration present within the boundary layer of colonies using laser doppler anemometry and high-speed microcinematography would give good descriptions of particle availability and movements; such a study may help resolve the nature of the forces responsible for particle motions.

The scale of turbulence in the flow tank cannot be greater than the diameter of the channel when the flow straighteners are removed (see Fig. 2); the characteristic length scale of turbulence in the field varies from site to site and can vary over an order of magnitude (Patterson, in prep.). Some of these flows have length scales far removed from that in the flow tank, making application of prey capture patterns seen in the tank to some field flows more problematic. More field measurements of flow in benthic microhabitats are needed to address this issue.

### *Deformation of filter elements*

Deformation of polyps does occur (Fig. 5, Table II) with increasing flow speed, and this helps explain the asymmetric nature of capture in the smooth flow. Due to

the low velocities below the level of the tentacles, polyps deform from shear stress acting on the oral disk (Patterson, unpub. data). Form drag of the anthocodia is likely to be important only at the higher flow speeds. The tentacular crown maintains its shape as the polyp is blown over, with the plane of the oral surface forming an increasing angle to the local direction of flow. The crown collapses into an inverted umbrella-like structure only at the highest flow speeds tested ( $30\text{--}40\text{ cm} \cdot \text{s}^{-1}$ ). Collapse is probably retarded by the stiffening effect on chevron-like arrays of spicules located at the attachment of the tentacles to the anthocodia. Surfaces of large colonies observed in the field occasionally displayed a cascading effect as the polyps were deformed in strong, unsteady flow ( $>50\text{ cm} \cdot \text{s}^{-1}$ ); waves of deformation passed through the columns in a manner similar to wind passing over a wheat field. A tropical octocoral, *Erythropodium caribaeorum*, possesses polyps of roughly the same size as *Alcyonium* and displays a similar behavior (pers. obs.).

Patterns of prey capture at the polyp level can be discerned using the same technique as for whole colony capture (Patterson, in prep.). The mode of prey capture seems to be direct interception (*sensu* Rubenstein and Koehl, 1977; Sebens and Koehl, 1984). The collapse of the upstream polyps changes the nature of the boundary layer flow and allows prey items to be injected below the tentacular canopy. While polyps deformed by the flow can still capture prey, they catch proportionately less as the flow speed increases (Patterson, in prep.).

### *Wake effects*

For Reynolds numbers in the range of  $100\text{--}10,000$ , particle entrainment in the recirculating wake of a bluff body can be invoked as a mechanism favoring prey capture in the lee of a suspension feeding organism. Prey capture might be augmented for downstream polyps by the following mechanisms: (1) higher concentrations of particles may occur in the eddying wake than in the free stream, (2) flow speeds over the filter elements may be reduced in the wake, possibly bringing the mean flow speed into some optimum range for the size and shape of the elements (Riedl and Forstner, 1968; Wainwright *et al.*, 1976), and (3) turbulence in the recirculating eddies may allow a greater probability of particle interception from enhanced diffusivity of particles and a more even distribution of particle concentrations immediately adjacent to the polyps.

The first hypothesis is not supported by the data in Table I. Particle concentrations in the wake of colonies are no higher than those in the free stream. This may be understood as follows. The density of planktonic organisms is usually close to that of water. Since the conservation of mass is equivalent to the conservation of volume in an incompressible fluid such as water, the volume of water entering the wake area must be equal to the amount of water leaving the wake. *A priori*, if a particle follows the streamlines of water movement, particle concentrations in the wake can never be higher than freestream values and should be equal. However, large changes in velocity are not accommodated by real particles which, due to their size, slight difference in density, and hence inertia relative to water molecules, deviate from the path of the water. Flow patterns experience sudden changes in speed and direction in and near the boundary of the wake. Vortices are typically shed in a 'von Kármán street' (Vogel, 1981) behind colonies at environmentally realistic flow speeds, and the radius of curvature of water motion in these areas can be on the order of a cm. Particles with sufficient inertia may not be able to make the turn into the wake area near the edge of the wake, and may instead continue downstream. The local pattern of accelerations and decelerations in the wake area may thus determine whether concentrations of particles in the wake will differ from those in the free stream. Unfortunately,

motions of particles at this size range are governed by both viscous and inertial effects (Spielman, 1977), and thus it is difficult to construct analytical models of particle behavior in such flows.

However, these results stand in contrast to laboratory work using laser doppler anemometry which can measure particle concentration with very fine spatial resolution (Bunimovich and Kudin, 1982). This technique has shown that part of the wake of a bluff body may experience an order of magnitude increase in particle concentration over the free stream (Lee and Srinivasan, 1978). The mechanism responsible for this phenomenon is unknown.

Particles dense enough to settle out over the depth of the wake on a time scale comparable to the average 'residence time' of a particle in the wake may be concentrated there (*cf.* gravitational deposition, Rubenstein and Koehl, 1977). This phenomena helps explain why rear windows on cars get dirtier than windshields (T. A. McMahon, Harvard University, pers. comm.), but may be of limited relevance to marine suspension feeders which usually consume prey with longer settling times (minutes) than typical wake residence times (seconds).

Direct interception is inversely dependent on flow velocity (Spielman, 1977; LaBarbera, 1984), but post-interception shear stresses on captured particles are often strong enough to dislodge them. The strength of attachment of nematocyst penetrants and threads is an unstudied area. The capture data reported here include successful captures only; J. Miles (Northeastern University, pers. comm.) has found that the loss of particles shows an increase with flow speed in the sea anemone *Metridium senile*. If a similar phenomenon occurs in *Alcyonium*, then the shift in capture may result from a shift in the location of an optimal local flow speed over the polyps. One might then expect the Reynolds number calculated for the most successful polyps in each set of experiments to be about the same, but this was not the case. Okamura (University of California, Berkeley, pers. comm.) has suggested that distributions of prey capture seen in the arborescent bryozoan *Bugula* may be due to a greater availability of particles to downstream branches as the flow speed increases. Upstream branches become increasingly less able to capture prey which then makes it further downstream. Also, 'conditioning' of the flow may also be important in this case, similar to that occurring in water movement through the alga *Gelidium* (Anderson and Charters, 1982). Upstream branches slow the mean flow speed while increasing levels of turbulence which can promote capture from turbulent diffusion.

While mean flow speeds are markedly lower in the wake, the level of turbulence increases (Schlichting, 1968); particles passing over the polyps in the wake have a higher probability of encountering a tentacle if momentum is being exchanged between layers of water near the colony. Turbulence enhances diffusivity of both motile and non-motile particles (Bird *et al.*, 1960). Hence, even if particle concentrations are lower in the wake at the highest speeds tested, turbulence will aid in prey capture. The disappearance of a downstream depletion of particles in the boundary layer of the colony due to migratory effects also probably results from the boundary layer becoming turbulent as the Reynolds number increases.

When the turbulence is increased in the free stream by moving the flow straighteners, the flow more closely resembles that found on the subtidal rock walls, and the effect disappears. Angular position on the colony is no longer a factor in predicting feeding success, for all polyps have an equal probability in capturing prey. Deformation still occurs, but the downstream gradient in particle concentration in the boundary layer of the colony does not occur. This seems to indicate that the depletion effect is the major factor governing distributions in the experiments with flow straighteners.

In the experiments with increased levels of turbulence, polyps further away from the substrate captured more prey only at the lowest speeds tested. This may underly

the observation that young colonies grow away from the substrate faster than they expand laterally. If the assumption is made that those polyps which eat more food have more polyps emerging adjacent to them from inside the colony, colonies should exhibit this growth pattern. In stagnant areas, colonies are taller and thinner relative to colonies in more well-mixed areas (Patterson, 1980). At higher flow speeds, the distribution again becomes asymmetric, this time with polyps at both the bottom and top of the colony catching relatively more prey. Since colonies of different heights displayed this bimodality, it seems likely that the pattern reflects the horseshoe vortex which forms on the upstream side of obstacles in flow near a substrate (Schlichting, 1968).

The observations above raise the interesting question of whether colony shape can be predicted from knowledge of whole colony capture patterns and *vice versa*. *Alcyonium* colonies display a variety of shapes including spherical geometries in hydraulically rough areas, and ellipsoids oriented at right angles to flow in smoother habitats. One might suspect that in a microhabitat where the direction of flow is predictable, colonies should grow fastest at the point where the flow speed around the colony is the greatest, at the 90° positions. Such a colony would eventually have an ellipsoidal shape. Colonies in a microhabitat subject to changing current direction would capture food in all directions and thus obtain a spherical geometry with time. However, these suspicions are technically difficult to test given the slow growth rate of the young colonies (Sebens, 1983c) and the difficulties of long-term monitoring and characterization of flow.

The mechanics of prey particle motion in the boundary layers of passive suspension feeders and the location and deformation of filter elements is of crucial importance to the feeding process. In the soft coral *Alcyonium*, the character of the flow carrying food past the filters can dramatically change the pattern of whole colony capture. Upon close inspection, many other passive suspension feeders may operate in a similar manner.

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